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EFFECT OF NURSERY CULTURE ON THE GROWTH OF WESTERN HEMLOCK SEEDLINGS DURING THE FIRST YEAR OF FIELD ESTABLISHMENT*

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ABSTRACT

The effects of nursery pretreatments, such as dormancy induction (photoperiod and moisture availability), two styroblock cavity sizes, and three dates of lifting and cold storage duration, on shoot length components were investigated in seedlings of western hemlock (Tsuga heterophylla (Raf.) Sarg.) during their first year of growth on two sites on Vancouver Island, B.C. Seedlings pretreated to short days combined with moisture stress and those lifted in November had very short shoots. Seedlings pretreated to long days and those lifted in March had the longest shoots. Because most stem units were preformed during bud development in the nursery, differences in stem unit length had a larger impact on shoot length than differences in number of stem units. Lammas growth was most frequent in seedlings from the smaller cavities and in those from the November and March lifts.

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INTRODUCTION

A variety of western hemlock (Tsuga heterphylla (Raf.) Sarg.) seedling stock types having different physiological and morphological characteristics can be produced by modifying nursery cultural practices (O'Reilly et al. 1989a, 1989b; Arnott et al. 1988; Grossnickle et al. 1988). A logical follow-up would be to see how different stock types perform under field conditions. To this end, we carried out a study of the phenology of flushing and shoot elongation, seedling morphology, and bud development of different seedling stock types of western hemlock growing on two adjacent sites, typical for the growing environment of the species on Vancouver Island. This paper summarizes some of the results on the effects of nursery pretreatment on shoot length components. Results of other parts of the field study will be reported in detail elsewhere and are summarized in the addendum to this paper.

MATERIALS AND METHODS

Seedling stock types

Western hemlock seedlings of mid-elevation (British Columbia Ministry of Forests Registered Seed Lot No. 3907; 48° 39' N, 123° 39' W, elevation, 760 m) seedlot from Vancouver Island were grown in BC/CFS styroblocks (PSB) (Beaver Plastics Ltd., Edmonton, Alta.) of small (PSB 313 abbreviated to S3) and large (PSB 415B abbreviated to S4) cavity diameters that were subjected to different dormancy induction and lift/storage treatment combinations (see Arnott et al. 1988). The seedlings were grown under 18 h day lengths until the dormancy induction treatments began. The dormancy induction treatments included short- (8 h) (SD) or long-day (18 h) (LD) photoperiods in combination with drought (D, dry) or no drought (W, wet) conditions that

began in mid-July, 1986 and ended 4 weeks later. Seedlings were grown under ambient day length conditions thereafter. The final treatment included three lifting dates/cold storage duration treatments that took place in mid-November, 1986 (lift N), mid-January (lift J) and mid-March (lift M) 1987, for a total of 24 nursery treatment combinations. Seedlings from lifts N and J were stored at 1°C in cold rooms at the Pacific Forestry Centre, Victoria until the final lift on March 18, 1987. All seedlings were transported to Nanaimo, B.C. where they were stored in a MacMillan Bloedel cold room (1°C) until planting.

Study area

The seedlings were planted in early April, 1987 on 2 adjacent sites at the Summit Main (SR5), Franklin River Division, MacMillan Bloedel Ltd. (Lat. 48° 55' N, Long. 124° 45', elev. 675 m). This area is within the windward submontane maritime wetter CWH variant (CWHbl) as described by Green et al. (1984). One site, facing northwest (NW), is classified as wet (hygrotope 5-6 trophotope B-C (burnt)) while the other is classified as dry (hygrotope 1-2, trophotope B-C (burnt)) and is of southeast (SE) aspect. Average slopes on these sites are about 60% and 40%, respectively.

Experimental design

The study area was layed out according to a split-plot factorial (randomized block) design, similar to that described in Kirk (1982). Each of the 24 nursery treatment combinations was represented by two replicates per block per site. Each replicate was assigned at random to a row plot; each row contained about 25 seedlings. Seedling spacing was at 2 m within rows and 1 m between rows. One of the two replicates per block was assigned at random for destructive sampling while the other was retained as a permanent plot.

Data collection

After shoot growth cessation in late September 1987, eight seedlings per row were sampled at random for study. A total of 1104 plants were examined; this was 48 less than planned because of seedling mortality.

Seedling shoot growth in the field in 1987 occurred through internodal elongation of stem units that originated from the overwintering bud, and from free and lammas growth. The stem units in the bud are predetermined as they were formed during nursery culture. Free growth occurred in the first season of field growth through production of new needle primordia followed by immediate internodal expansion. Lammas growth occurred through the premature flushing of the new bud that was formed in the same season. It was not possible to distinguish needles produced during free growth from those present in the overwintering bud. However, a good estimate could be made of these numbers because numbers of needle primordia in the overwintering bud were recorded at the end of the nursery experiment (O'Reilly et al. 1989b). The lammas portion of the shoot was easy to identify by the presence of bud scales on the new shoot in addition to those of the new overwintering bud. Also, some free growth commonly takes place as the lammas bud elongates; all growth distal to the lammas bud scales was considered as lammas growth despite this fact. The 1987 shoot was divided into two portions for the purpose of this study, the predetermined-free and the lammas growth sections.

The following data were recorded from the 1987 shoot of each seedling: (1) total shoot length; (2) length of lammas shoot; numbers of needles or stem units[5] (NSU) in the (3) pre-determined-free (4) and lammas growth sections of shoot;

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[5] A stem unit is "an internode, together with the node and nodal appendages at its distal extremity" (Doak 1935). Needles and lammas bud scales are stem units of interest in this study; both types underwent internodal expansion.

and (5) numbers of bud scales at base of the lammas shoot. New variables calculated from these data included: (6) total NSU, i.e. (3) + (4) + (5); and (7) lammas NSU, i.e. (4) + (5). Stem unit length (SUL) was calculated for the (8) whole shoot and for the (9) predetermined-free and (10) lammas portions of the shoot by dividing shoot length by NSU for the appropriate portion.

Data analysis

Data were analysed according to a modified version of the split-plot factorial (randomized block) design as outlined in Kirk (1982). The Spssx MANOVA procedure (Spssx Inc. 1986) using unique sums of squares was employed in all analyses. The influence of a(the) factor(s) (e.g. site) and the interaction(s) of that(those) factor(s) with site were tested using the site by factor(s) by block within site as the error term (e.g. site by block within site), thus generating 16 error terms for each variable analysed.

RESULTS

Shoot length is determined by its components, NSU and SUL. Therefore, the effect of nursery pretreatment and site on these components are considered before addressing their combined effect on shoot length. Only mean pretreatment and site effects that are most representative of the data are presented in the figures.

Number of stem units and lammas growth

Planting site ($p<0.001$) and the nursery pretreatments - moisture ($p<0.01$), day length ($p<0.05$), cavity size ($p<0.05$), lift ($p<0.05$) - and the interactions of day length by lift ($p<0.01$) and site by day length by lift ($p<0.01$) significantly influenced final NSU. However, the results for all except site effects are confounded by differences

among pretreatments in preformed NSU.

Differences among nursery pretreatments in NSU on the NW site within lift N seedlings (Fig. 1A) closely paralleled final needle primordium numbers recorded in the nursery study (O'Reilly et al. 1989b). Seedlings pretreated to moisture stress and long days had the least number of needle primordia at planting, the effect of the former being greater than the latter. Seedlings from the SDW pretreatment had the greatest number of primordia at planting.

Seedlings from the SE site usually produced the most NSU, but this varied with nursery preconditioning. Seedlings from SDD had no free growth or produced few new stem units during free growth across all lifts and on both sites. Few new stem units were produced during free growth in seedlings pretreated to SDW from any lift-storage precondition on the NW site, but those from lifts J and M produced some free growth stem units on the warmer SE site. Seedlings of both moisture levels pretreated to LD showed a similar pattern across all lifts and both sites. Within the November-lifted stock, seedlings pretreated to LD showed a much different pattern than those that received SD. Seedlings pretreated to LD within lift N produced many new stem units during free growth on the SE site, but few on the NW site. Seedlings from other lifts within this pretreatment produced many stem units during free growth.

Seedlings from S4 had greater NSU than those from S3, mainly due to differences in fixed NSU (O'Reilly et al. 1989b). On average, seedlings from S4 had 10 needle primordia more at planting than those from S3. However, there were large differences in NSU between lifts for seedlings from S3 at the end of the field season, but small differences in those from S4 (Fig. 1A). These differences occurred mainly due to the greater amounts of free growth stem units produced in S3 seedlings from lifts J and M and

in those from S4 within lift N. Differences were relatively consistent across the pretreatments within each lift.

The frequency of lammas growth varied with site and nursery pretreatment (Fig. 2). The highest frequency of lammas shoots was in seedlings from lifts N and M, especially in those from S3. Differences in lammas shoot frequencies combined with variation in lammas NSU are reflected in final NSU values (Fig. 1B). Note the general increase in NSU in seedlings from lift M and in those from S3 within the J and M lifts. Seedlings from the smaller cavities produced the least NSU, especially those from lift N.

Stem unit length

Stem unit length varied significantly due to nursery pretreatments - lift ($p<0.001$), day length ($p<0.05$) and day length by moisture stress ($p<0.05$). Lifting date had a large and consistent effect on mean SUL, but the influence of dormancy induction pretreatment was variable (Fig. 3). Plants from lift N had the shortest SUL. Seedlings pretreated to LD had larger mean SUL than those from SD. Plants of both moisture levels in the nursery within LD had similar SUL but those stressed within SD had very short SUL. Planting site by day length effects appear substantial, although these were not significant ($p<0.09$). Site means are presented because they had an important effect on final shoot length when combined with the influence of NSU. Plants from the SE site had larger SUL when pretreated to LD and SDD, while those pretreated to SDW showed the reverse pattern. There were no significant differences in SUL between the lammas and fixed-free portions of the shoot.

Shoot length

Field height growth was significantly affected by the nursery pretreatments - lifting date ($p<0.001$), day length

($p<0.01$), moisture ($p<0.05$), cavity size ($p<0.05$) and day length by site ($p<0.01$), and moisture by day length ($p<0.05$).

Seedlings from SDD conditions in the nursery had the shortest shoots due to the short SUL and low NSU (Fig. 4A). Shoot length in those pretreated to SDW were much greater than those pretreated to SDD because they had more stem units in their overwintering buds (O'Reilly et al. 1989b) and had greater SUL. Number of free growth stem units was not a major factor for seedlings pretreated to SD. Shoot length in SDW seedlings was similar on both sites, but this was achieved in different ways. Seedlings on the NW site had greater SUL but had fewer stem units than those on the SE site. Seedlings from both moisture levels of the LD pretreatments had similar final shoot length. Shoot length of plants from the NW site of this pretreatment was similar to those from SDW. The greater growth achieved in the LD pretreated plants on the SE site was mainly due to the greater SUL, although NSU produced during free and lammas growth also contributed.

Differences in shoot length due to cavity size resulted from differences in NSU only. Seedlings from the larger cavities had greater preformed NSU (O'Reilly et al. 1989b). However, seedlings from S3 produced more free growth and lammas growth than those from S4 (Fig. 4B).

Lammas growth had the largest effect on seedlings from S3, especially in those pretreated to LD. This effect of LD was not apparent in the NSU (Fig. 1) and lammas frequency data (Fig. 2); the much greater SUL combined with greater NSU resulted in substantial shoot length differences in these seedlings. Changes in final shoot length due to lammas growth were generally greatest in seedlings from lifts N and M and on the SE site, especially in those from SDD on that site.

DISCUSSION

Shoot length is determined by the number of stem units and stem unit length; the former is considered far more important than the latter in this regard (Cannell et al. 1976). These components of shoot length are thought to vary independently (Cannell 1979), although this may not always be the case (Kremer and Larson 1983; Bongarten 1986; Hallgren and Helms 1988). Most NSU in seedlings of western hemlock were preformed, i.e. they were initiated by activity of the apical meristem during nursery growth (O'Reilly et al. 1989b). In contrast, SUL is determined by activity of the intercalary meristems located between the needle primordia and subsequent cell elongation. Therefore, final SUL is determined by processes that become activated mostly during field growth.

Variation in NSU due to nursery pretreatment in the portion of the shoot that elongated before lammas growth took place (Fig. 1A) largely agreed with that measured in the nursery study (O'Reilly et al. 1989b). The influence of lifting date mostly reflected differences in NSU produced during free growth because date of lifting had little effect on final primordium numbers in the nursery study (O'Reilly et al. 1989b). In addition, planting site had a significant influence on NSU across all lifts, site effects being largest within the LD November-lifted stock.

Seedlings from the short days and moisture stress pretreatment had short SUL, with little difference due to planting site. These seedlings produced few additional stem units during free growth, and combined with their very short SUL, produced very short shoots. Seedlings with a large number of needles are most susceptible to moisture stress during elongation (Hallgren and Helms 1988), perhaps accounting for the shorter SUL in seedlings from SDW growing on the warmer SE site (Fig. 3). Furthermore, seedlings from

the SD pretreatment, especially those from SDW of lift M, flushed their buds more rapidly than other seedlings (O'Reilly et al, unpubl.). Flushing rates were most rapid on the SE site, perhaps making them susceptible to moisture stress during early shoot elongation. The 1987 growing season was warm and dry at the study sites[6]. Also, competition for metabolites among elongating stem units may have resulted in the shorter SUL on the SE site where some free growth took place, a hypothesis first proposed by Kremer and Larson (1983) to explain the negative correlation found between NSU and SUL in seedlings of Pinus banksiana Lamb. The large number of preformed needles in seedlings from SDW (O'Reilly et al. 1989b) combined with adequate SUL allowed good shoot growth in the field. Seedlings pretreated to LD in this study had longer shoots achieved through larger SUL as well as greater NSU produced during free growth and lammas growth, probably owing to the higher physiological quality of these plants.

Differences in final shoot length due to cavity size were attributable to differences in NSU only. The larger NSU that were predetermined in seedlings from S4 than in those from S3 (O'Reilly et al. 1989b) explained most of these differences. Similarly, plant spacing in the nursery had a large effect on height growth up to 3 years after field planting in seedlings of Douglas fir (Pseudotsuga menziesii Mirb. Franco) (van den Driessche 1984).

Interestingly, lammas growth was most frequent in seedlings from S3 and in those from lifts N and M. Because of the superior physiological quality and greater vigour of lift M stock (Arnott et al. 1988), it is not surprising that they had a high frequency of lammas shoots. The relatively high frequency of lammas growth in the November-lifted stock probably was related to the physiological and developmental

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[6]Data on file, Forestry Canada, Victoria, B.C.

characteristics of these seedlings. Seedlings from this lift flushed much later in the field than those from other lifts (O'Reilly et al, unpubl.), probably because its dormancy intensity was very high at time of planting (Arnott et al. 1988). In addition, these plants began bud development at an earlier date than those from other lifts, and they often resumed growth after producing a few bud scales only (O'Reilly et al., unpubl.). The late release from dormancy combined with earlier date of bud formation perhaps made these plants prone to lammas growth. Lammas shoot length was very short in these seedlings because they produced few lammas stem units and had short SUL. The high frequency of lammas growth on seedlings from S3 is more difficult to explain. Seedlings from S3 were smaller but had greater apical dominance than those from S4 (O'Reilly et al. 1989a); such plants may have been more responsive to environmental changes that induce lammas growth.

The confounding effect of seedling size at planting on shoot growth except for that of cavity size has not been addressed in this paper. Seedlings pretreated to long days were about 25% taller and were much more heavily branched (O'Reilly et al. 1989a) than those pretreated to short days. Moisture stress had a smaller effect on seedling size while lifting date had a negligible effect on these characteristics. Seedlings treated to SDW grew adequately in the field relative to planting height, but these plants had the advantage of having many preformed stem units.

CONCLUSIONS

Spring lifting followed by immediate field planting provide the best shoot growth during the first year of field establishment in western hemlock seedlings. Seedlings subjected to long days during dormancy induction in the nursery achieved better shoot growth after outplanting than

those treated to short days. Moisture stress in the nursery had little effect on shoot growth in the field of seedlings from the LD pretreatment but greatly reduced shoot growth of those from the SD pretreatment. Because most stem units were preformed during bud development in the nursery, differences in SUL had a larger impact on shoot length than differences in NSU. Lammas growth was most frequent in seedlings from the smaller cavities and in those from the November and March lifts.

ADDENDUM

In addition to the findings presented in this paper, the other most significant results of the study of seedling growth in the first growing season in the field were:

1. Spring lifting (in early March) followed by immediate field planting produced the best growth and survival of western hemlock seedlings.

2. Day length pretreatments in the nursery had no effect on survival but influenced stem diameter, shoot and needle growth. Seedlings treated to short days in July/August had greater relative growth rates than those treated to long days but plants from the latter pretreatment had longer shoots at the end of the growing season. Seedlings pretreated to long days also had the greatest diameter and needle growth.

3. Short days in the nursery advanced flushing dates in the field and delayed the development of terminal buds at the end of the first growing season.

4. Moisture stress pretreatment reduced survival, had no effect on bud development and had variable effects on growth

rates.

5. Hemlock seedlings flushed earlier and grew more rapidly on the warmer SE site than those on the cooler NW site. Bud development was more rapid on the NW site, perhaps because of the higher frequency of free growth and lammas growth on that site. However, final values for all variables differed little between sites.

6. Seedlings lifted too early (in November) and placed in cold storage flushed later and had fewer leaf primordia in the buds formed at the end of the first growing season, than those seedlings that were lifted in March.

7. Survival, diameter increment and needle growth were lower in seedlings from the smaller cavities (PSB 313) than in those from the larger cavities (PSB 415B). The phenology of flushing, shoot elongation and bud development was similar in seedlings from the two cavity sizes, except for the rapid increase in shoot elongation that took place in late August in seedlings from the larger containers growing on the SE site.

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Fig. 1. Mean number of stem units before (A) and after (B) lammas growth has occurred during the first year of field establishment on two sites in seedlings of western hemlock that were subjected to different nursery pretreatment combinations. Means are taken across other pretreatments or sites not included in that hierarchy. N, J, and M indicate November, January and March lifts, respectively. SDD, SDW, LDD and LDW refer to short-day dry, short-day wet, long-day dry and long-day wet pretreatment combinations, respectively. NW and SE indicate north-west and south-east sites, respectively. S3 and S4 refer to small and large styroblock cavity sizes, respectively. Vertical lines indicate 1 SE.

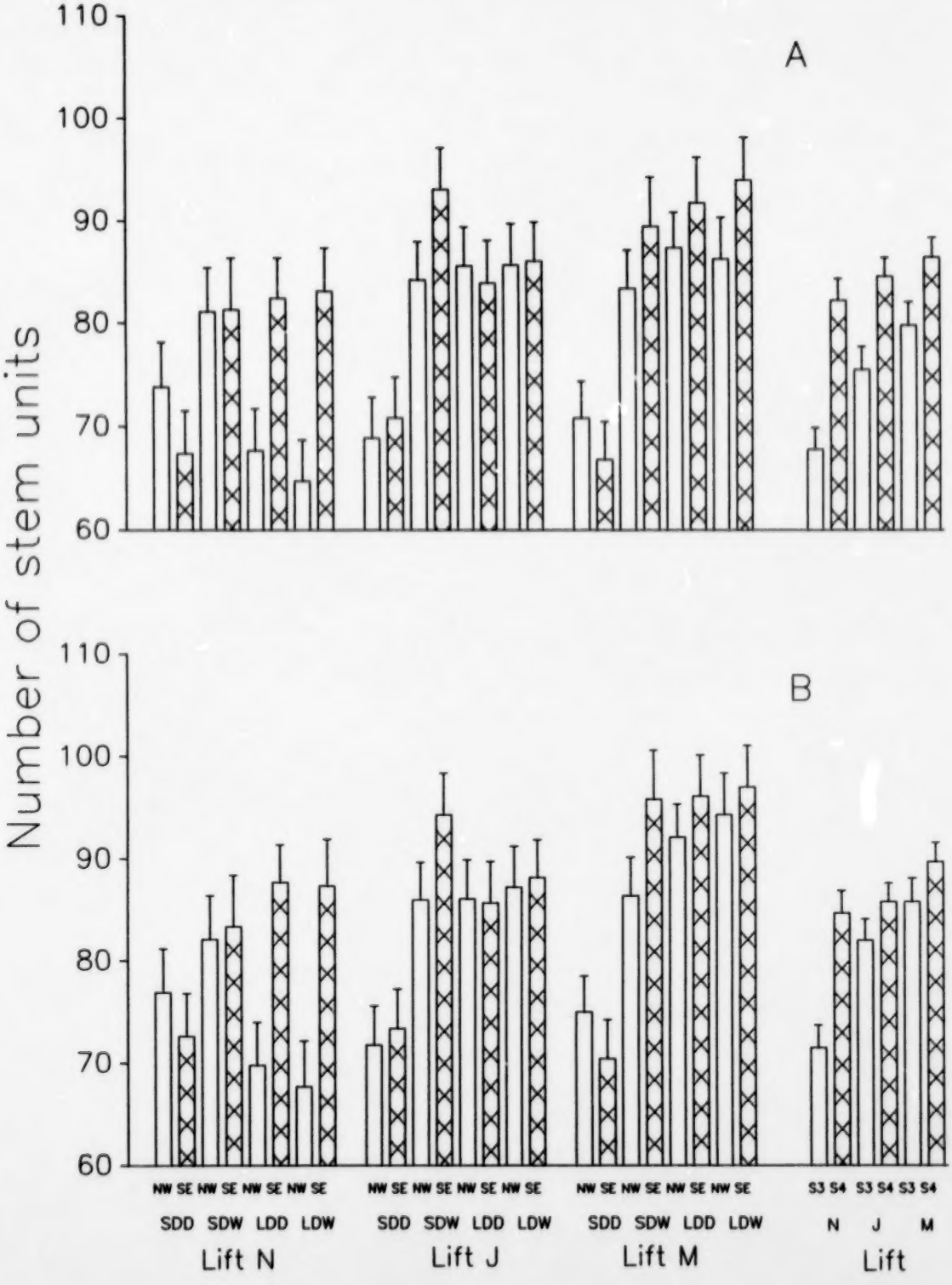

A
B
Number of stem units
110
100
90
80
70
60
NW SE NW SE NW SE NW SE
SDD SDW LDD LDW
Lift N
Lift J
Lift M
S3 S4 S3 S4 S3 S4
N J M
Lift

Fig. 2. Lammas growth frequencies (%) during the first year of field establishment on two sites in seedlings of western hemlock that were subjected to different nursery pretreatment combinations. Means are taken across other pretreatments or sites not included in that hierarchy. N, J, and M indicate November, January and March lifts, respectively. SDD, SDW, LDD and LDW refer to short-day dry, short-day wet, long-day dry and long-day wet pretreatment combinations, respectively. NW and SE indicate north-west and south-east sites, respectively. S3 and S4 refer to small and large styroblock cavity sizes, respectively.

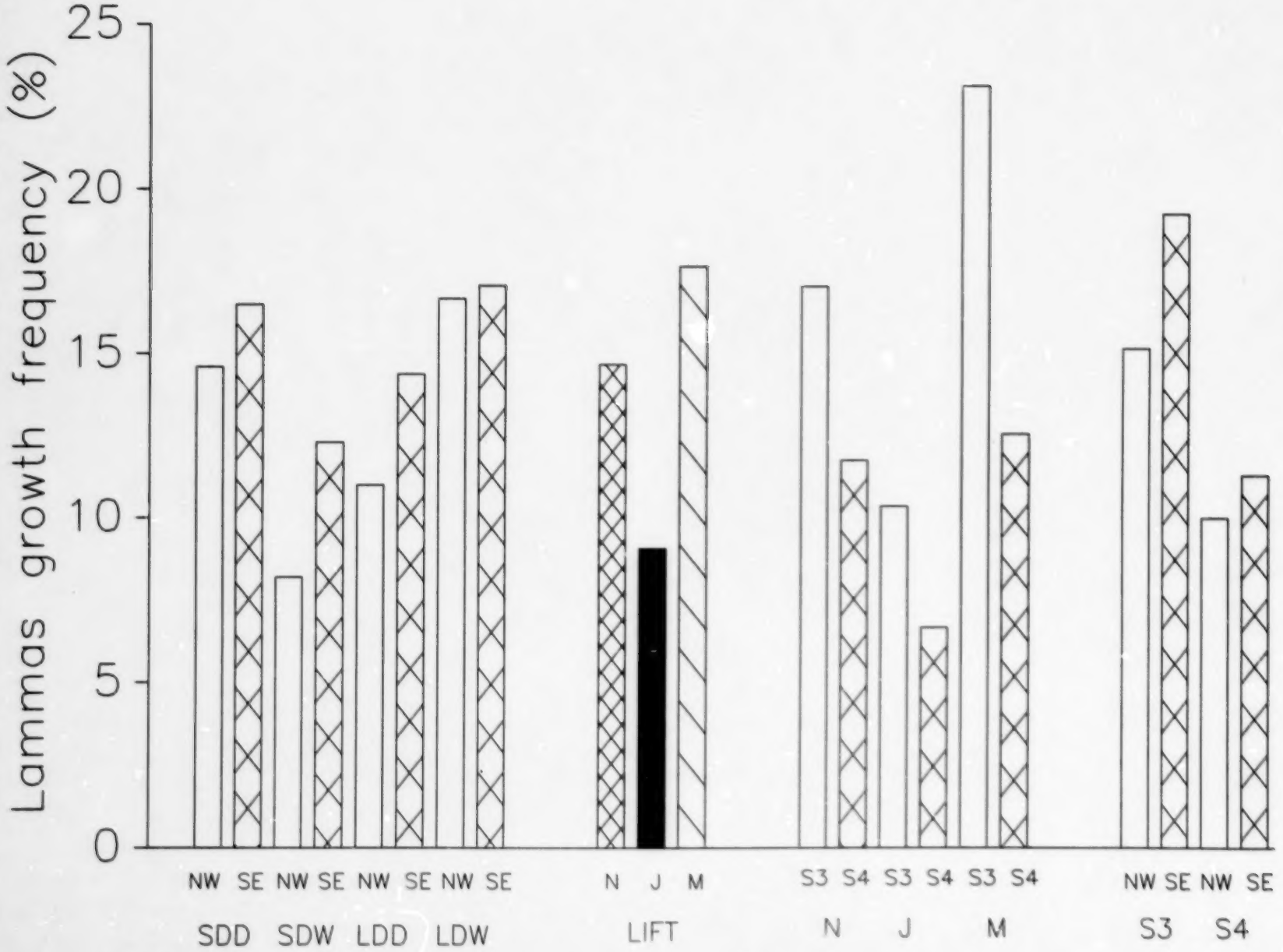

Lammas growth frequency (%)
25
20
15
10
5
0
NW SE NW SE NW SE NW SE
SDD SDW LDD LDW
N J M
LIFT
S3 S4 S3 S4 S3 S4
N J M
NW SE NW SE
S3 S4

Fig. 3. Stem unit length at the end of shoot growth during the first year of field establishment on two sites in seedlings of western hemlock that were subjected to different nursery pretreatment combinations. Means are taken across other pretreatments or sites not included in that hierarchy. N, J, and M indicate November, January and March lifts, respectively. SDD, SDW, LDD and LDW refer to short-day dry, short-day wet, long-day dry and long-day wet pretreatment combinations, respectively. NW and SE indicate north-west and south-east sites, respectively. Vertical lines indicate 1 SE.

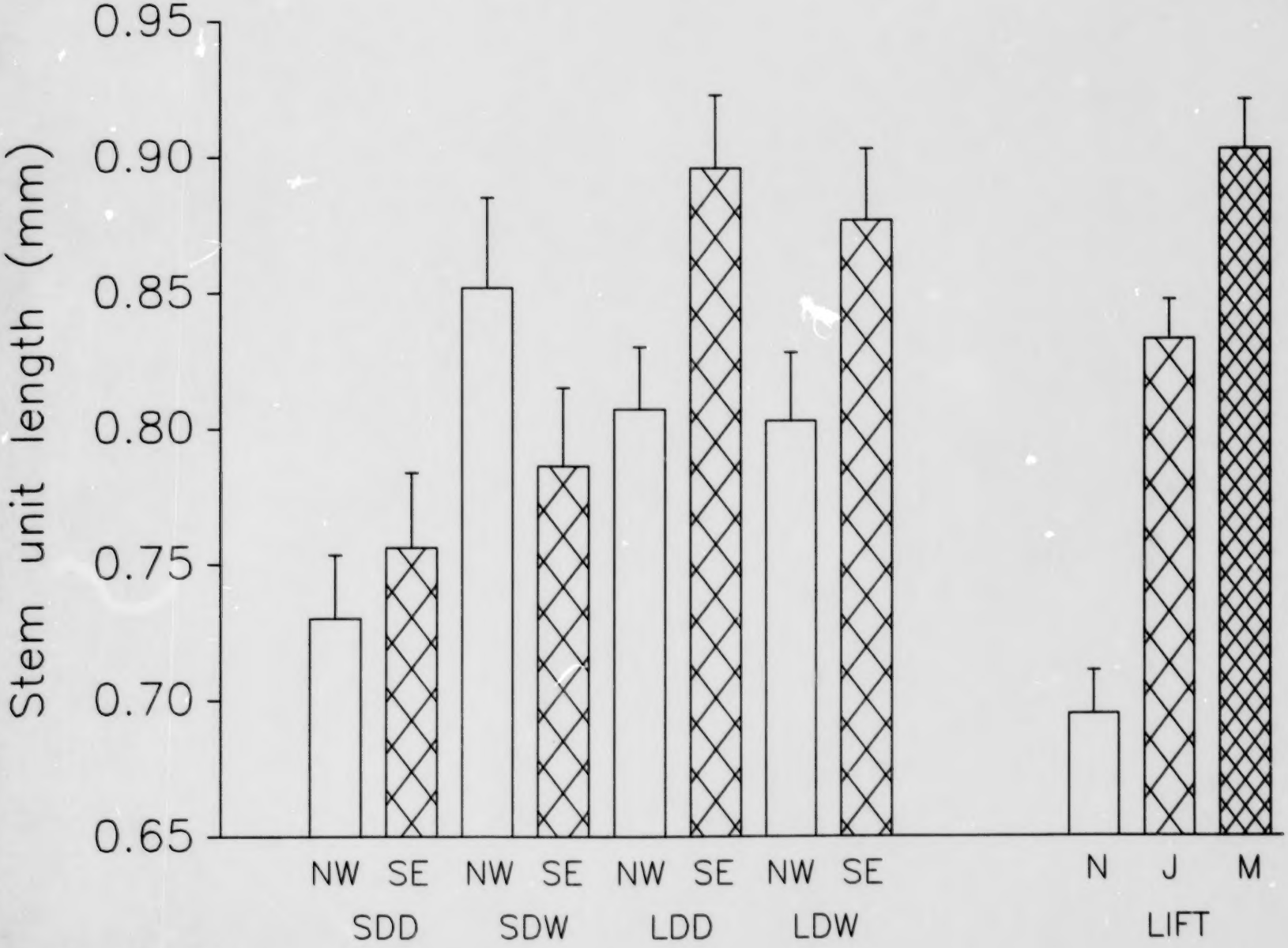
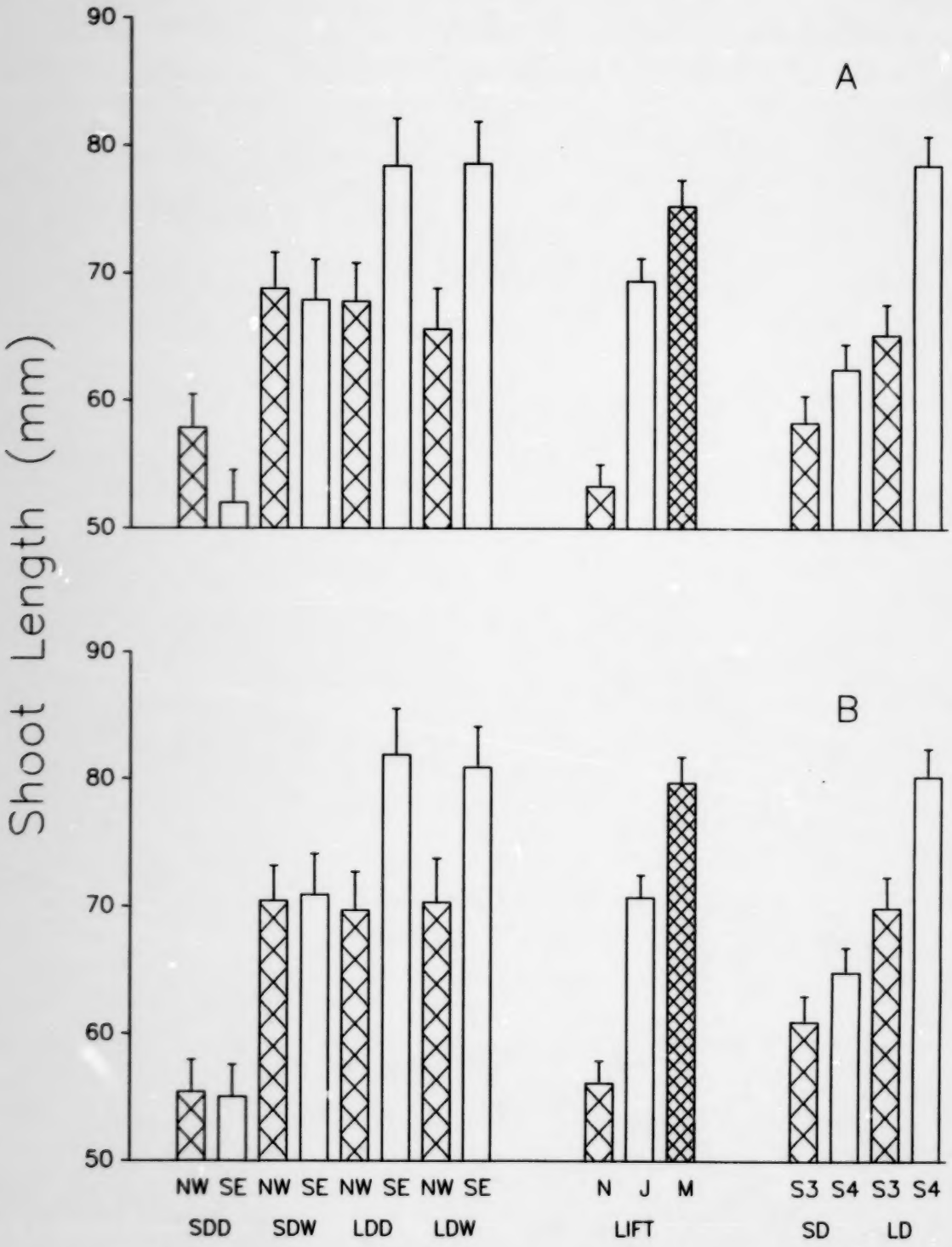

Stem unit length (mm)
0.95
0.90
0.85
0.80
0.75
0.70
0.65
NW
SE
NW
SE
NW
SE
NW
SE
N
J
M
SDD
SDW
LDD
LDW
LIFT

Fig. 4. Shoot length before (A) and after (B) lammas growth has occurred during the first year of field establishment on two sites in seedlings of western hemlock that were subjected to different nursery pretreatment combinations. Means are taken across other pretreatments or sites not included in that hierarchy. N, J, and M indicate November, January and March lifts, respectively. SDD, SDW, LDD and LDW refer to short-day dry, short-day wet, long-day dry and long-day wet pretreatment combinations, respectively. SD and LD refer to short- and long-day pretreatments, respectively. NW and SE indicate north-west and south-east sites, respectively. S3 and S4 refer to small and large styroblock cavity sizes, respectively. Vertical lines indicate 1 SE.


Shoot Length (mm)
90
80
70
60
50
A
B
NW SE NW SE NW SE NW SE
SDD SDW LDD LDW
N J M
LIFT
S3 S4 S3 S4
SD LD